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Published in:
Journal of Experimental Biology

J. exp. Biol. **134**, 173–183 (1988)
Printed in Great Britain © *The Company of Biologists Limited 1988*

INDOOR FLIGHT EXPERIMENTS WITH TRAINED KESTRELS

I. FLIGHT STRATEGIES IN STILL AIR WITH AND WITHOUT ADDED WEIGHT

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Accepted 22 July 1987

SUMMARY

Two kestrels, a male and a female, were trained to fly over 50 and 125 m in a windless corridor. Both distances were flown with or without dead weights attached to the feet during 13 flight sessions for each bird. Added weight was either 0·3 N (31 g lead) or 0·6 N (61 g). Each session was devoted to one distance and one flight weight category. Flight duration was automatically recorded at the landing points and at four positions along the track. Gliding bouts were hand-clocked and flight altitudes were estimated with the aid of sidewall markings.

An analysis was made of 1226 flights by the female over a total of 100 km, and 1017 flights by the male over 84·6 km.

Different flight strategies were observed under the different experimental situations, and were compared with model predictions for optimal speeds.

In the unloaded situations the birds flew at velocities close to the maximum range speed. Under load, speeds were lower and close to the predicted speeds for minimum power when 0·6 N was added to the weight.

INTRODUCTION

Kestrels spend most of their energy upon flight. The hunting flight of the kestrel (*Falco tinnunculus*) consists of short bouts of flight at wind speed against the wind over a fixed position relative to the ground (windhovering: Videler, Weihs & Daan, 1983) and of short flights from one such position to the next. Flights must also be made between the nest and the hunting ground, with and without prey. During the breeding season, male kestrels fly for up to 5 h each day (Masman, 1986).

The mechanical power required for level flight at a uniform speed is the sum of the power needed to produce thrust (proportional to the flight speed cubed) and the power needed to produce lift (inversely proportional to speed). The relationship between mechanical power and speed can be roughly estimated using semi-empirical models (e.g. Tucker, 1974; Greenewalt, 1975; Pennycuick, 1975). These

Key words: kestrel, flight strategies, added weight.

power–speed curves are U-shaped and predict one flight speed for minimum power (U_{mp}) and a higher speed where the amount of work per unit distance covered is at a minimum (the maximum range speed U_{mr}). Both optimal speeds increase with an increase of body mass, because the induced power increases as the weight squared. The speeds mentioned here are relative to the air surrounding the bird. In the field, speed over the ground is difficult to measure and can deviate substantially from air speed, depending on wind velocity and direction.

In this paper we have investigated the costs of straight, forward flight, with and without prey, using two haggard (mature, wild) birds, trained to fly up and down a long corridor, with and without added weight. The investigation was carried out under windless conditions, where steady periodic wing motions could give the bird an approximately constant air and ground speed. The experimental conditions were arranged so that the bird was completely free to choose its flight speed and so that the mass and position of the added weight closely resembled those of a prey item. The subsequent paper (Videler, Groenewegen, Gnodde & Vossebelt, 1988) deals with the kinematics of flapping flight under loaded and unloaded conditions. Energy expenditure during the corridor flights was measured by combining food balance and indirect calorimetric techniques and is published elsewhere in an ecological context (Masman & Klaassen, 1987).

MATERIALS AND METHODS

Falconry

Two wild adult birds, one female ('Kes') and one male ('Jowie'), were trapped, kept and trained using falconry techniques (Glasier, 1982). The birds had a short leather anklet ('aylmeri' in falconers' terms) fitted around each leg, secured by a metal eyelet. A piece of nylon string (about 25 cm long) with a knot at one end, threaded through the eyelets, was used to secure the bird to its perch or to the glove during transport. For the added-weight experiments, the aylmeri were made of lead, weighing either 0·3 N (mass 31 g) or 0·6 N (61 g) per pair. These weights represent the range of weights of prey items of kestrels (Masman, Gordijn, Daan & Dijkstra, 1986).

Morphometric data are collected in Table 1. The body masses indicated are 20–30 g lower than the mass at the moment of capture. At this lower level the birds were in good condition and keen to fly. Daily exercise started after working hours in the 142 m long, 3·4 m wide and 2·4 m high corridor of the Biological Centre in Haren. Each bird had to fly up and down between the gloves of two falconers. Food (small bits of minced mouse) was offered at the gloves after 80 % of the landings (randomly distributed). The body mass of the animals was measured just before a training session. The daily food ration was equal to the difference between the body mass given in Table 1 and the mass at the start of the session. Only very small pieces of mouse were offered at the glove to get as many flights as possible out of the ration. The body mass was checked after the flight sessions before the birds were returned to their perches. A session was devoted to one distance of either 50 or 125 m. The flights

Table 1. *Summarized data of 2243 recorded corridor flights of one female and one male kestrel*

Flight session no.	1	2	3	4	5	6	7	8	9	10	11	12	13
Female Kes: wingspan 0·72 m; wing area 0·0598 m^2; body area 0·0102 m^2.													
Distance (m)	50	50	125	125	125	50	50	125	125	50	50	125	125
Added weight (N)	0	0	0	0	0	0·3	0·3	0·3	0·3	0·6	0·6	0·6	0·6
Bird body mass													
before session (g)	186·0	181·1	186·8	188·8	182·2	179·7	178·3	179·6	180·6	177·7	180·5	178·5	177·4
after session (g)	198·0	195·7	198·6	195·8	197·8	198·0	198·8	197·0	197·6	195·8	197·2	196·8	196·2
Average body mass (g)	192	189	193	193	190	189	189	189	185	187	189	188	186
Number of flights	156	128	56	78	92	106	112	106	80	96	112	54	50
Distance covered (km)	7·8	6·4	7	9·75	11·5	5·3	5·6	13·25	10	4·8	5·6	6·75	6·25
Average speed ($m\,s^{-1}$)	7·74	7·78	8·70	8·68	9·03	7·72	7·56	8·74	8·82	7·46	7·17	8·06	8·17
S.D.	0·15	0·16	0·24	0·19	0·20	0·10	0·21	0·12	0·13	0·56	0·09	0·08	0·17
Cruising speed ($m\,s^{-1}$)	9·35	9·26	9·58	9·58	9·96	9·01	8·85	9·62	9·84	8·70	8·20	8·68	8·86
S.D.	0·42	0·25	0·28	0·35	0·49	0·08	0·23	0·29	0·26	0·76	0·13	0·12	0·15
Male Jowie: wingspan 0·70 m; wing area 0·0567 m^2; body area 0·0104 m^2.													
Distance (m)	50	50	50	125	125	50	50	125	125	50	50	125	125
Added weight (N)	0	0	0	0	0	0·3	0·3	0·3	0·3	0·6	0·6	0·6	0·6
Bird body mass													
before session (g)	155·3	155·0	154·7	153·1	153·1	152·4	154·3	152·9	156·2	153·6	154·4	155·0	153·6
after session (g)	164·5	166·4	168·2	168·7	169·1	168·6	168·3	167·4	168·2	168·7	168·1	167·2	168·3
Average body mass (g)	160	161	163	161	161	161	161	160	162	162	161	161	161
Number of flights	84	46	90	72	72	78	74	103	100	70	120	58	50
Distance covered (km)	4·2	2·3	4·5	9	9	3·9	3·7	12·875	12·5	3·5	6·0	7·25	6·25
Average speed ($m\,s^{-1}$)	7·38	7·58	7·43	8·52	8·50	7·28	7·21	8·30	8·39	7·11	6·99	7·89	8·09
S.D.	0·17	0·18	0·21	0·20	0·16	0·22	0·14	0·14	0·15	0·14	0·11	0·14	0·14
Cruising speed ($m\,s^{-1}$)	9·01	9·09	8·85	9·17	9·73	8·70	8·55	9·26	9·36	8·33	8·26	8·68	8·96
S.D.	0·24	0·16	0·23	0·26	0·26	0·15	0·21	0·20	0·24	0·20	0·13	0·21	0·19

were numbered successively, even-numbered flights in the opposite direction to odd-numbered flights.

Registration of flight data

During the experiments flight data were recorded on a Sinclair ZX 81 computer, connected to a quartz clock for precise timekeeping. Electronic switches in the gloved left hand of the falconers clocked landing and take-off times with an accuracy of 0·01 s. The number of flights, the duration of each crossing and the flight direction could be deduced from these data. At four positions along the flight track, infrared-light-sensitive cells, mounted on the floor under infrared lights in the ceiling, recorded the instant of passing of a bird. These extra registration points subdivided the 50 and 125 m flights into segments of 10 and 25 m, respectively (illustrated in Table 2: Kes, session 1 and 3). The birds always changed from flapping flight to gliding on approaching the end of the track. The instant of this change was hand-clocked for each flight and stored in the memory. These data provided accurate estimates of gliding times. A more detailed registration of the starting and landing parts of the 125 m flights was obtained by concentrating the positions of the infrared-light-sensitive cells at one end of the corridor 10 m apart (Table 2: Kes, session 5).

Markings on the side wall of the corridor made it possible to make a rough estimate of the flight altitude. Velocities were calculated by dividing the distance between two registration points by the time taken to cover that distance. For each flight, cruising speed was estimated to be the speed between two central registration points (between 20 and 30 m, and 50 and 75 m, for 50 m and 125 m flights, respectively).

Data were obtained from 13 flight sessions for each bird. Each bird flew both distances during at least two sessions with added weights of 0, 0·3 and 0·6 N. Statistical analysis was made using SPSS software.

RESULTS

Kes flew 1226 recorded flights over a total distance of 100 km: 42·45 km without added weight, 34·15 km with 0·3 N and 23·4 km carrying 0·6 N. Jowie covered 84·6 km in 1017 flights: 29 km without extra weight, 32·6 km with 0·3 N, and 23 km with 0·6 N. Summarized flight data for the 13 sessions for each bird are presented in Table 1.

General description of flight patterns

The flight behaviour of the kestrels in the corridor was extremely stereotyped. Flapping flight was used to descend from the falconer's hand (at a height of about 1·8 m), and then used to proceed about two-thirds of the way to the other falconer. This was followed by a glide that ended with a short swoop up to the glove.

Flight altitude was mainly between 0·3 and 0·4 m. Kes flew between 0·4 and 0·8 m during sessions 1 and 4, during 21 % of the flights of session 8 and 54 % of session 9. Occasional flights during the other sessions were also higher than 0·4 m. Jowie had a few high flights in sessions 4, 9, 12 and 13 and considerable numbers in sessions 1

Table 2. *Examples of averaged data, collected during three flight sessions with a trained female kestrel (Kes) without added weight*

Flight session 1

Start — Finish

1·55 s	1·13 s	1·07 s	1·12 s	1·60 s
(s.d. = 0·04)	(s.d. = 0·02)	(s.d. = 0·05)	(s.d. = 0·03)	(s.d. = 0·07)
	Flapping		Gliding	
6·45 m s^{-1}	8·85 m s^{-1}	9·35 m s^{-1}	8·93 m s^{-1}	6·24 m s^{-1}
0–10	10–20	20–30	30–40	40–50 m

Flight session 3

Start — Finish

3·21 s	2·49 s	2·61 s	2·61 s	3·47 s
(s.d. = 0·08)	(s.d. = 0·05)	(s.d. = 0·08)	(s.d. = 0·08)	(s.d. = 0·26)
	Flapping		Gliding	
7·79 m s^{-1}	10·00 m s^{-1}	9·58 m s^{-1}	9·58 m s^{-1}	7·20 m s^{-1}
0–25	25–50	50–75	75–100	100–125 m

Flight session 5

Start — Finish

1·56 s	1·12 s	1·03 s	0·97 s	4·53 s	0·98 s	1·05 s	1·12 s	1·55 s
(s.d. = 0·04)	(s.d. = 0·02)	(s.d. = 0·01)	(s.d. = 0·02)	(s.d. = 0·21)	(s.d. = 0·05)	(s.d. = 0·04)	(s.d. = 0·03)	(s.d. = 0·06)
			Flapping				Gliding	
6·41 m s^{-1}	8·93 m s^{-1}	9·71 m s^{-1}	10·31 m s^{-1}	9·93 m s^{-1}	10·20 m s^{-1}	9·52 m s^{-1}	8·93 m s^{-1}	6·45 m s^{-1}
0–10	10–20	20–30	30–40	40–85	85–95	95–105	105–115	115–125 m

Session 1: 156 flights over 50 m, space between registration points is 10 m.
Session 3: 56 flights over 125 m, space between registration points is 25 m.
Session 5: 92 flights over 125 m, the registration points are concentrated, 10 m apart, in one end of the corridor.

(40 %), 5 (10 %), 6 (26 %) and 7 (12 %). There is no noticeable effect of differences in altitude on flight durations.

Differences between flights in the even and odd directions

The duration of the even flights was not statistically different from that of the flights in the opposite direction in 23 of the 26 sessions, but was different in three sessions (Kes 3 and 7, Jowie 7). During these sessions we did not notice any obvious difference in behaviour between the flights in either direction, except for Kes 3. In this case the difference was caused by a difference in the mean duration of the last 25 m. On the even flights, duration was 3·34 s (S.D. = 0·07) and in the opposite direction it was 3·62 s (S.D. = 0·31). The high standard deviation of the odd cases reveals erratic behaviour of the bird during the last 25 m of the flight. We noticed on a few occasions that the final swoop was not along a straight line but followed a curved glide sideways if the hand of the falconer was not in the correct position. But it also happened without reasons obvious to the falconers. During session 3 something in the appearance of one falconer must have disturbed Kes and caused the difference in landing behaviour.

The effect of the differences between even- and odd-numbered flights on the session averages are small compared to the effects of added weight or different distances.

Comparison of flight patterns

With a load of 0 or 0·3 N, Kes flew about 0·3–0·4 m s^{-1} faster than Jowie (Table 1). Over a distance of 125 m, with a load of 0·6 N, this speed difference vanished completely. Jowie's cruising speed during session 13 was even higher than the equivalent speeds during sessions 12 and 13 of Kes.

The average speed of both birds over 125 m was 1 m s^{-1} faster than over 50 m. Cruising speed was of course relatively less influenced by starting and landing and was 0·5 m s^{-1} faster during 125 m flights.

In both birds flight speed tended to decrease with added weight. Addition of 0·3 N reduced cruising speed by an average of 0·4 m s^{-1} and lowered the velocity by an average of 0·3 m s^{-1}. The added weight seemed to affect Kes more strongly than Jowie. Table 1 shows that, despite the general trend, the velocities of Kes during sessions 8 and 9 with 0·3 N added weight are higher instead of lower than during sessions 3 and 4. (The difference between sessions 8 and 3 is not significant; the differences between sessions 9 and 3, 9 and 4, and 8 and 4 are significant.) The standard deviations of the average and cruising speeds of session Kes 10 are notably higher than all the other standard deviations in Table 1. This session was the first one for Kes with an added weight of 0·6 N. A detailed look at her 96 flights shows a peculiar change of behaviour after flight 38. The standard deviations show the usual order of magnitude, if the data for the first 38 flights are separated from the others. Kes obviously started off very fast, even faster than during a session without added weight. The durations of the second group of flights are similar to those of session 11, to the other 50 m/0·6 N session of Kes and to sessions 10 and 11 of Jowie.

Gliding behaviour

The birds glided without losing height. They decelerated at the same flight level to a point about 5 m in front of the falconer where the final swoop to the glove started. The glide altitude was recorded in 1705 cases. 85·6 % of the glides were between 0·3 and 0·4 m, 13·7 % between 0·4 and 0·8 m and in 11 cases the altitude was higher than 0·8 m. The glides were usually straight and uninterrupted (70 %), 25 % were interrupted once and 5 % two or more times by a few wing beats.

Tables 3 and 4 show how gliding duration decreased with weight increase. Kes reduced her gliding times more drastically than Jowie, from 36 % down to about 10 % of the total flight duration. The rate of deceleration was estimated from data of the odd-numbered flights of Kes's session 5 where the registration points were concentrated at the end of the flight track. We selected four flights with uninterrupted glides at one altitude over slightly more than 30 m distance. The velocity decreases between 95 and 105 m were 0·810, 0·875, 0·972 and 0·842 $m\,s^{-1}$ in the four cases, giving deceleration values of 0·77, 0·82, 0·91 and 0·85 $m\,s^{-2}$, respectively, with an average of 0·84 $m\,s^{-2}$. From this deceleration value a lift/drag ratio of 11·7 can be calculated assuming that there was no height loss (lift equals weight and drag equals mass times deceleration).

DISCUSSION

The average cruising speeds during unloaded 125 m flights, 9·45 $m\,s^{-1}$ for Jowie and 9·71 $m\,s^{-1}$ for Kes, are close to the U_{mr} velocities predicted by the models of Greenewalt (1975), Pennycuick (1975) and Tucker (1974). The predicted values for Jowie and Kes are, respectively, 9·6 and 10·3 (Greenewalt), 10·7 and 11·2 (Tucker) and 11·0 and 11·6 $m\,s^{-1}$ (Pennycuick). The minimum power velocity (U_{mp}) predicted by the models is on average 2 $m\,s^{-1}$ lower than the speed of the birds. During the 50 m flights, the cruising speeds are about 0·5 $m\,s^{-1}$ lower. This agrees with Rayner's (1979) prediction and is probably an attempt to minimize the costs of acceleration during take-off and deceleration before landing.

The models predict an increase of U_{mr} and U_{mp} with increased weight, but instead the birds decreased their speed. The velocities with 0·6 N added weight are close to the predicted values for U_{mp} instead of U_{mr}. The cruising speeds with 0·6 N load over 125 m average 8·82 $m\,s^{-1}$ for Jowie and 8·77 $m\,s^{-1}$ for Kes. The predicted U_{mp} values are 8·3 and 8·6 (Greenewalt), 8·2 and 8·5 (Tucker) and 7·6 and 7·8 $m\,s^{-1}$ (Pennycuick) for Jowie and Kes, respectively. The average cruising velocities are compared with predictions from Greenewalt's model in Fig. 1. The birds appear to change their strategy from cruising at U_{mr} to U_{mp} when flying under loaded conditions. The three models predict an average increase of power of 33 % for Jowie and 21 % for Kes. The metabolic energy required for unloaded flight in the corridor of three kestrels, including Kes and Jowie, has been estimated to be about 14 W (Masman & Klaassen, 1987). This figure combined with the model predictions indicates that the 0·6 N added-weight flight of Jowie requires about 19 W of

Table 3. *Indoor flight data for two kestrels, distance 50 m, with and without added weight*

Flight session no.	Added weight (N)	Flight duration (S.D.) (s) Distance covered 0–10 m	10–20 m	20–30 m	30–40 m	40–50 m	Total distance 0–50 m	Gliding bout (s)	Average speed ($m\,s^{-1}$)
Kes									
1	**0**	**1·55** (0·04)	**1·13** (0·02)	**1·07** (0·05)	**1·12** (0·03)	**1·60** (0·07)	**6·46** (0·12)	**2·36** (0·22)	**7·74**
2	**0**	**1·58** (0·04)	**1·14** (0·03)	**1·08** (0·03)	**1·09** (0·03)	**1·52** (0·05)	**6·43** (0·13)	**2·03** (0·24)	**7·78**
6	**0·3**	**1·62** (0·04)	**1·16** (0·02)	**1·11** (0·01)	**1·09** (0·02)	**1·50** (0·04)	**6·48** (0·09)	**1·82** (0·15)	**7·72**
7	**0·3**	**1·66** (0·04)	**1·19** (0·03)	**1·13** (0·03)	**1·10** (0·02)	**1·53** (0·07)	**6·61** (0·14)	**1·66** (0·17)	**7·56**
10	**0·6**	**1·74** (0·11)	**1·23** (0·11)	**1·15** (0·11)	**1·12** (0·07)	**1·46** (0·10)	**6·70** (0·48)	**0·95** (0·16)	**7·46**
Flights 1–38		1·61 (0·04)	1·09 (0·05)	1·03 (0·06)	1·02 (0·03)	1·33 (0·05)	6·07 (0·17)	1·13 (0·21)	8·23
39–96		1·81 (0·05)	1·30 (0·01)	1·22 (0·05)	1·17 (0·01)	1·52 (0·03)	7·03 (0·09)	0·91 (0·13)	7·11
11	**0·6**	**1·80** (0·05)	**1·28** (0·02)	**1·22** (0·02)	**1·17** (0·02)	**1·50** (0·04)	**6·97** (0·09)	**0·95** (0·15)	**7·17**
Jowie									
1	**0**	**1·62** (0·03)	**1·16** (0·02)	**1·11** (0·03)	**1·15** (0·04)	**1·74** (0·08)	**6·77** (0·16)	**2·64** (0·25)	**7·38**
2	**0**	**1·58** (0·07)	**1·15** (0·02)	**1·10** (0·02)	**1·14** (0·03)	**1·64** (0·08)	**6·60** (0·16)	**2·68** (0·27)	**7·58**
3	**0**	**1·63** (0·04)	**1·18** (0·03)	**1·13** (0·03)	**1·16** (0·06)	**1·65** (0·08)	**6·73** (0·20)	**2·32** (0·28)	**7·43**
6	**0·3**	**1·73** (0·04)	**1·19** (0·03)	**1·15** (0·02)	**1·14** (0·03)	**1·68** (0·07)	**6·89** (0·11)	**2·41** (0·20)	**7·28**
7	**0·3**	**1·75** (0·05)	**1·22** (0·03)	**1·17** (0·03)	**1·15** (0·03)	**1·64** (0·07)	**6·93** (0·13)	**2·06** (0·17)	**7·21**
10	**0·6**	**1·81** (0·04)	**1·25** (0·04)	**1·20** (0·03)	**1·17** (0·03)	**1·60** (0·06)	**7·03** (0·14)	**1·77** (0·14)	**7·11**
11	**0·6**	**1·83** (0·04)	**1·28** (0·02)	**1·21** (0·02)	**1·18** (0·02)	**1·65** (0·06)	**7·14** (0·12)	**1·77** (0·12)	**6·99**

Table 4. *Indoor flight data for two kestrels, distance 125 m, with and without added weight*

Flight session no.	Added weight (N)	Flight duration (s.d.) (s) Distance covered 0–25 m	25–50 m	50–75 m	75–100 m	100–125 m	Total distance 0–125 m	Gliding bout (s)	Average speed ($m\,s^{-1}$)
Kes									
3	**0**	**3·21** (0·08)	**2·49** (0·05)	**2·61** (0·08)	**2·61** (0·08)	**3·47** (0·26)	**14·38** (0·39)	**5·17** (0·35)	**8·70**
4	**0**	**3·25** (0·04)	**2·55** (0·05)	**2·61** (0·10)	**2·68** (0·10)	**3·38** (0·10)	**14·40** (0·31)	**4·32** (0·44)	**8·68**
8	**0·3**	**3·38** (0·08)	**2·61** (0·05)	**2·60** (0·08)	**2·60** (0·08)	**3·10** (0·09)	**14·30** (0·20)	**3·69** (0·33)	**8·74**
9	**0·3**	**3·35** (0·04)	**2·58** (0·05)	**2·54** (0·07)	**2·55** (0·08)	**3·15** (0·08)	**14·17** (0·21)	**3·51** (0·47)	**8·82**
12	**0·6**	**3·67** (0·05)	**2·90** (0·03)	**2·88** (0·04)	**2·81** (0·04)	**3·25** (0·06)	**15·52** (0·15)	**1·50** (0·21)	**8·06**
13	**0·6**	**3·63** (0·06)	**2·85** (0·07)	**2·82** (0·05)	**2·74** (0·07)	**3·24** (0·07)	**15·30** (0·35)	**1·68** (0·31)	**8·17**
Jowie									
4	**0**	**3·39** (0·06)	**2·60** (0·07)	**2·56** (0·07)	**2·65** (0·10)	**3·47** (0·09)	**14·67** (0·33)	**4·09** (0·42)	**8·52**
5	**0**	**3·43** (0·05)	**2·64** (0·06)	**2·57** (0·07)	**2·58** (0·08)	**3·46** (0·11)	**14·71** (0·28)	**3·76** (0·32)	**8·50**
8	**0·3**	**3·64** (0·13)	**2·77** (0·05)	**2·70** (0·06)	**2·64** (0·05)	**3·31** (0·08)	**15·06** (0·26)	**2·77** (0·27)	**8·30**
9	**0·3**	**3·57** (0·08)	**2·73** (0·06)	**2·67** (0·07)	**2·62** (0·04)	**3·30** (0·08)	**14·90** (0·27)	**2·73** (0·31)	**8·39**
12	**0·6**	**3·68** (0·07)	**2·89** (0·08)	**2·88** (0·07)	**2·85** (0·09)	**3·46** (0·07)	**15·85** (0·29)	**2·43** (0·27)	**7·89**
13	**0·6**	**3·67** (0·09)	**2·84** (0·07)	**2·79** (0·06)	**2·76** (0·06)	**3·38** (0·08)	**15·45** (0·27)	**2·29** (0·28)	**8·09**

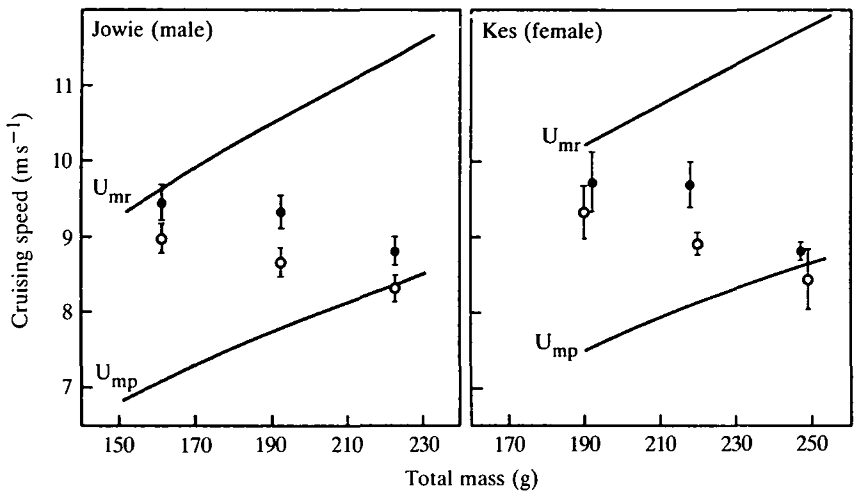

Fig. 1. Average cruising velocities with standard deviations during flights over 125 m (closed circles) and 50 m (open circles) of a male and a female kestrel with different flight weights. Data are compared with predictions for maximum range (U_{mr}) and minimum power (U_{mp}) speeds from Greenewalt's (1975) model (lines).

metabolic power and that of Kes about 17 W. The models predict that the power increase would be twice as high (Jowie 61 %, Kes 48 %) if the birds were to follow the U_{mr} strategy. This would require sustained metabolic energy expenditures of more than 20 W for both birds. Our results suggest that a weight increase of one-third of the body mass forces kestrels to fly slower and to increase the energy for flight to a level probably close to the limit of available aerobic energy. Session 10, where Kes suddenly changed her flight speed after flight 38, suggests that we witnessed a real change of strategy and not just a gradual decline of speed due to fatigue under the heavy load. A reduction in speed and an increase in wingloading force the birds to decrease their gliding distance if they do not want to lose height drastically. The kestrels use their kinetic energy to cover the last part of the track at low cost, but they do not use the possibility of losing height as well as speed to increase the gliding distance.

Spedding (1987*a*,*b*) flew a kestrel down a 36 m long corridor and visualized the wake during gliding and flapping flight. His bird was approximately the same size as Kes and flew at about 7 $m\,s^{-1}$ in midflight, following the trend to fly slower over a shorter distance. Flight and gliding height were between 0·36 and 0·45 m, similar to that seen in our experiments and higher than the bird's semispan. Spedding (1987*a*) concluded that the ground effect during gliding at this height is probably of limited importance. The qualitative vortex wake structure during flapping flight at the same height is, according to Spedding (1987*b*), probably not significantly influenced by ground effect. Videler *et al.* (1983) used Tucker & Parrott's (1970) equations to calculate the maximum lift/drag ratio for a kestrel of 207 g. Their value of 11·1 almost coincides with our maximum value estimate of 11·7 for Kes.

We are grateful to Dr N. Fox for introducing JJV to scientific falconry and to Hanneke Videler for the initial training of the birds. We thank the inhabitants of the Biological Centre for accepting the inconvenience of a closed corridor.

Financial support of the Hasselblad Foundation is gratefully acknowledged.

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